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(1104L) Plants introduction
class="introduction"

Seedless
plants, like
these
horsetails
(*Equisetum*
sp.), thrive in
damp,
shaded
environment
s under a tree
canopy
where
dryness is
rare. (credit:
modification
of work by
Jerry
Kirkhart)



Not all plants make seeds! In fact, the first plants to evolve did not reproduce through seeds. Today, seedless plants represent only a small fraction of the plants in our environment; the average person has heard of and recognizes mosses and ferns. Three hundred million years ago however, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposition created large deposits of coal that we mine today.

Current evolutionary thought holds that all plants—green algae as well as land dwellers—are monophyletic; that is, they are descendants of a single common ancestor that was undoubtedly aquatic. The evolutionary transition from water to land imposed severe constraints on plants. They had to develop strategies to avoid drying out, to disperse reproductive cells in air, for structural support, and for capturing and filtering sunlight. While seed plants developed adaptations that allowed them to populate even the most arid habitats on Earth, full independence from water did not happen in all plants. Most seedless plants still require a moist environment. There must have been some advantage to growing on the land though - can you think of what that might have been?

(1104L) Early Plant Life

By the end of this section, you will be able to:

- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize the land
- Describe the timeline of plant evolution and the impact of land plants on other living things

The Plant Kingdom constitutes large and varied groups of organisms. There are more than 300,000 species of plants documented by science. Most biologists also consider green algae to be plants, although others exclude all algae from the plant kingdom. The reason for this disagreement stems from the fact that only green algae, the **Charophytes**, share common characteristics with land plants (such as using chlorophyll *a* and *b* plus carotene in the same proportion as plants). These characteristics are absent in other types of algae.

Note:

Evolution Connection

Algae and Evolutionary Paths to Photosynthesis

Some scientists consider all algae to be plants, while others assert that only the Charophytes belong in the kingdom Plantae. These divergent opinions are related to the different evolutionary paths to photosynthesis selected for in different types of algae. While all algae are photosynthetic—that is, they contain some form of a chloroplast—they didn't all become photosynthetic via the same path.

The ancestors to the green algae became photosynthetic by endosymbiosing a green, photosynthetic bacterium about 1.65 billion years ago. This event is described in the Endosymbiotic Theory, which also explains the presence of mitochondria in all eukaryotes, including plants. After acquiring the chloroplast, this algal line evolved into the Charophytes, and eventually into the modern mosses, ferns, gymnosperms, and angiosperms. In contrast, the other algae—red, brown, golden, stramenopiles, and so on—all became photosynthetic by secondary, or even tertiary, endosymbiotic events; that is, they endosymbiosed cells that had already endosymbiosed a cyanobacterium. These latecomers to

photosynthesis are parallels to the Charophytes in terms of autotrophy, but they did not expand to the same extent as the Charophytes, nor did they colonize the land. Although there is a lot of facts that support the Endosymbiotic Theory, you should not just accept it and move on! Doesn't this sound improbable? Aren't you curious as to what facts could support such a crazy-sounding theory? It may not be an emphasis in the class you are taking now, but I encourage you to take a look at the factual evidence [here](#).

Plant Adaptations to Life on Land

The Challenges to Life on Land

As organisms adapted to life on land, they had to contend with several challenges in the terrestrial environment. Water is the solvent of life and neither we, nor plants (nor anything!) could survive without it. The cell's interior is a watery soup in which most small molecules dissolve and diffuse, and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for an organism exposed to air. Even when parts of a plant are close to a source of water, the aerial structures are likely to dry out. Water also provides buoyancy to organisms. On land, plants need to develop structural support because (obviously) air does not give the same lift as water. The organism is also subject to bombardment by mutagenic radiation, because air does not filter out ultraviolet rays of sunlight. Additionally, the male gametes must reach the female gametes using new strategies, because swimming only possible through water. Therefore, both gametes and zygotes must be protected from desiccation. The successful land plants developed strategies to deal with all of these challenges. Not all adaptations appeared at once. Some species never moved very far from the aquatic environment, whereas others went on to conquer the driest environments on Earth.

The Advantages to Life on Land

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. Water acts as a filter, altering the spectral quality of light absorbed by the photosynthetic pigment chlorophyll. Second,

carbon dioxide is more readily available in air than in water, since it diffuses faster in air. Third, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened plant life. This situation changed as animals emerged from the water and fed on the abundant sources of nutrients in the established flora. In turn, plants developed strategies to deter predation: from spines and thorns to toxic chemicals.

Early land plants, like the early land animals, did not live very far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is called tolerance. Many mosses, for example, can dry out to a brown and brittle mat, but as soon as rain or a flood makes water available, mosses will absorb it and are restored to their healthy green appearance. Another strategy is to colonize environments with high humidity, where droughts are uncommon. Ferns, which are considered an early lineage of plants, thrive in damp and cool places such as the understory of temperate forests. Later, plants moved away from moist or aquatic environments using resistance to desiccation, rather than tolerance. These plants, like cacti, minimize the loss of water to such an extent they can survive in extremely dry environments.

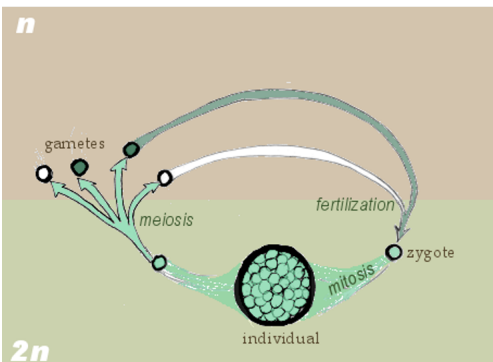
The most successful adaptation solution was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in roots and shoots. The evolution of a waxy cuticle and a cell wall with lignin also contributed to the success of land plants. These adaptations are noticeably lacking in the closely related green algae—another reason for the debate over their placement in the plant kingdom.

Alternation of Generations

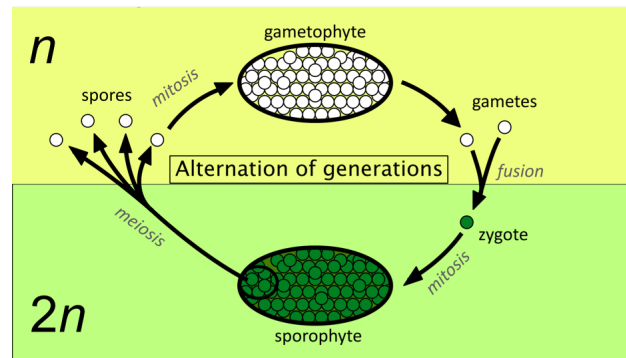
Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages ([\[link\]](#)). This is very different from the animal life cycle that humans have because our haploid stage

(sperm and egg) remain single celled and do not have an independent existence outside of the body like the plant haploid stage (called the "gametophyte")

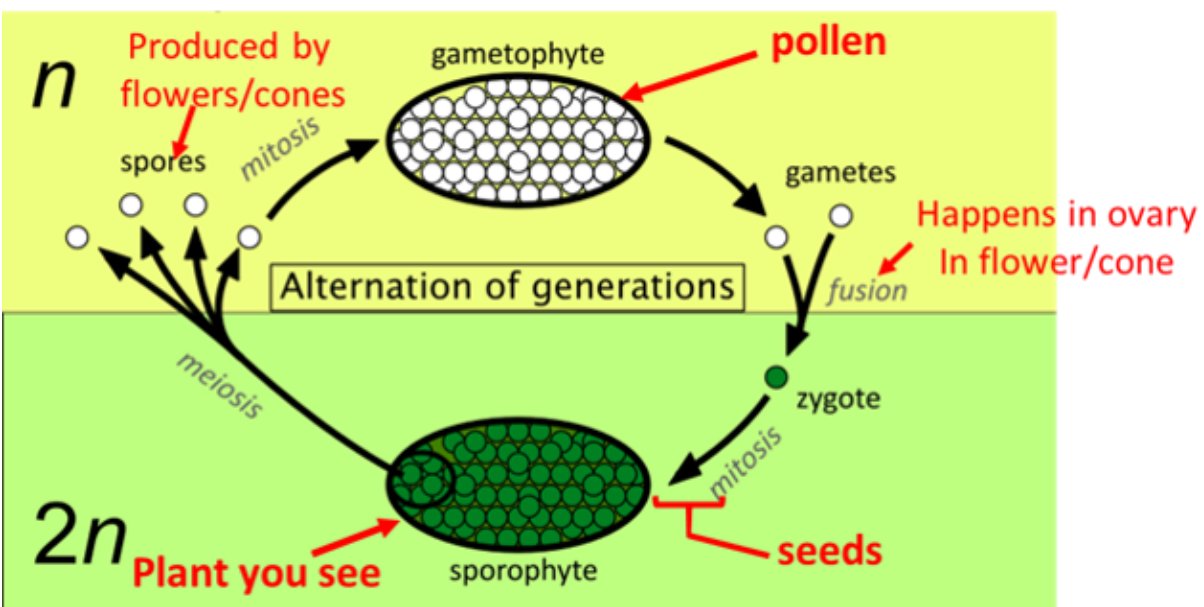
Animal life cycle



Plant life cycle



Unlike animals, plants have a multicellular haploid phase of their lifecycle. Phases labeled *2n* are diploid and those labeled *n* are haploid. (credit: Jeff Mahr, adapted from Wikipedia)



Locations of some commonly recognized plant structures in the plant alternation of generation life cycle

Sporangia in Seedless Plants

The sporophyte of seedless plants is diploid and results from the fusion of two gametes, forming the zygote. From the zygote grows the sporophyte, which has sporangia (singular, sporangium): organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel,” as it is a reproductive sac that contains spores [\[link\]](#). Inside the multicellular sporangia, the diploid **sporocytes**, or mother cells, produce haploid spores by meiosis, where the $2n$ chromosome number is reduced to $1n$ (note that many plant sporophytes are polyploid: for example, durum wheat is tetraploid, bread wheat is hexaploid, and some ferns are 1000-ploid). The spores are later released by the sporangia and disperse in the environment.



Spore-producing sacs called sporangia grow at the ends of long, thin stalks in this photo of

the moss *Esporangios bryum*.
(credit: Javier Martin)

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as **sporopollenin**. This complex substance is characterized by long chains of organic molecules related to fatty acids and carotenoids: hence the yellow color of most pollen. Sporopollenin is unusually resistant to chemical and biological degradation. In seed plants, which use pollen to transfer the male sperm to the female egg, the toughness of sporopollenin explains the existence of well-preserved pollen fossils. Sporopollenin was once thought to be an innovation of land plants; however, the green algae *Coleochaetes* forms spores that contain sporopollenin.

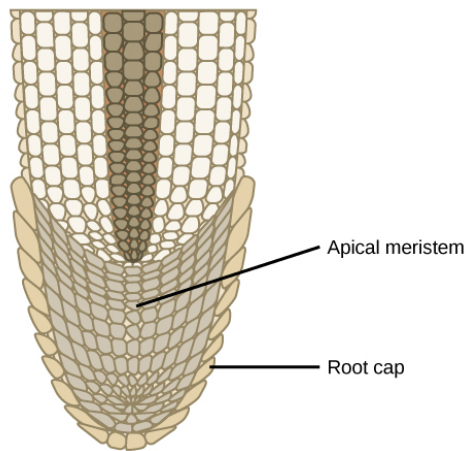
Gametangia in Seedless Plants

Gametangia (singular, gametangium) are structures observed on multicellular haploid gametophytes. In the gametangia, precursor cells give rise to gametes by mitosis. The male gametangium (**antheridium**) releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the **archegonia**: the female gametangium. The embryo develops inside the archegonium as the sporophyte. Gametangia are prominent in seedless plants, but are very rarely found in seed plants.

Apical Meristems

Shoots and roots of plants increase in length through rapid cell division in a tissue called the apical meristem, which is a small zone of cells found at the

shoot tip or root tip ([link](#)). The apical meristem is made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the organism. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter of tree trunks.



Addition of new cells in a root occurs at the apical meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

Additional Land Plant Adaptations

As plants adapted to dry land and became independent from the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow more than a few inches off the ground, competing for light on these low mats. By developing a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). In small plants such as single-celled algae, simple diffusion suffices to distribute water and nutrients throughout the organism. However, for plants to evolve larger forms, the evolution of vascular tissue for the distribution of water and solutes was a prerequisite. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals absorbed from the soil up to the shoot, while phloem transports food derived from photosynthesis throughout the entire plant. A root system evolved to take up water and minerals from the soil, and to anchor the increasingly taller shoot in the soil.

In land plants, a waxy, waterproof cover called a cuticle protects the leaves and stems from desiccation. However, the cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. To overcome this, stomata or pores that open and close to regulate traffic of gases and water vapor appeared in plants as they moved away from moist environments into drier habitats.

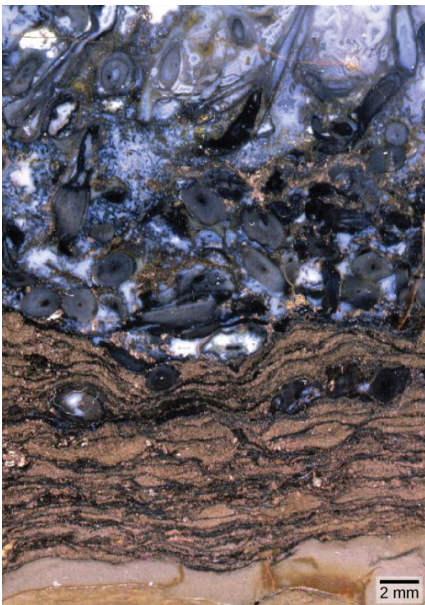
Water filters ultraviolet-B (UVB) light, which is harmful to all organisms, especially those that must absorb light to survive. This filtering does not occur for land plants. This presented an additional challenge to land colonization, which was met by the evolution of biosynthetic pathways for the synthesis of protective flavonoids and other compounds: pigments that absorb UV wavelengths of light and protect the aerial parts of plants from photodynamic damage.

Plants cannot avoid being eaten by animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can also cause severe diseases and even death, thus discouraging predation. Humans have used many of these compounds for centuries as drugs, medications, or spices. In contrast, as plants co-evolved

with animals, the development of sweet and nutritious metabolites lured animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been enlisting animals to be their helpers in this way for hundreds of millions of years.

Evolution of Land Plants

No discussion of the evolution of plants on land can be undertaken without a brief review of the timeline of the geological eras. The early era, known as the Paleozoic, is divided into six periods. It starts with the Cambrian period, followed by the Ordovician, Silurian, Devonian, Carboniferous, and Permian. The major event to mark the Ordovician, more than 500 million years ago, was the colonization of land by the ancestors of modern land plants. Fossilized cells, cuticles, and spores of early land plants have been dated as far back as the Ordovician period in the early Paleozoic era. The oldest-known vascular plants have been identified in deposits from the Devonian. One of the richest sources of information is the Rhynie chert, a sedimentary rock deposit found in Rhynie, Scotland ([link](#)), where embedded fossils of some of the earliest vascular plants have been identified.



(a)



(b)

This Rhynie chert contains fossilized material from vascular plants. The area inside the circle contains bulbous underground stems called corms, and root-like structures called rhizoids. (credit b: modification of work by Peter Coxhead based on original image by “Smith609”/Wikimedia Commons; scale-bar data from Matt Russell)

Paleobotanists distinguish between **extinct** species, as fossils, and **extant** species, which are still living. The extinct vascular plants, classified as zosterophylls and trimerophytes, most probably lacked true leaves and roots and formed low vegetation mats similar in size to modern-day mosses, although some trimerophytes could reach one meter in height. The later genus *Cooksonia*, which flourished during the Silurian, has been extensively studied from well-preserved examples. Imprints of *Cooksonia* show slender branching stems ending in what appear to be sporangia. From the recovered specimens, it is not possible to establish for certain whether *Cooksonia* possessed vascular tissues. Fossils indicate that by the end of the Devonian period, ferns, horsetails, and seed plants populated the landscape, giving rising to trees and forests. This luxuriant vegetation helped enrich the atmosphere in oxygen, making it easier for air-breathing animals to colonize dry land. Plants also established early symbiotic relationships with fungi, creating mycorrhizae: a relationship in which the fungal network of filaments increases the efficiency of the plant root system, and the plants provide the fungi with byproducts of photosynthesis.

Note:**Career Connection****Paleobotanist**

How organisms acquired traits that allow them to colonize new environments—and how the contemporary ecosystem is shaped—are fundamental questions of evolution. Paleobotany (the study of extinct plants) addresses these questions through the analysis of fossilized

specimens retrieved from field studies, reconstituting the morphology of organisms that disappeared long ago. Paleobotanists trace the evolution of plants by following the modifications in plant morphology: shedding light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Fossils are formed when organisms are trapped in sediments or environments where their shapes are preserved. Paleobotanists collect fossil specimens in the field and place them in the context of the geological sediments and other fossilized organisms surrounding them. The activity requires great care to preserve the integrity of the delicate fossils and the layers of rock in which they are found.

One of the most exciting recent developments in paleobotany is the use of analytical chemistry and molecular biology to study fossils. Preservation of molecular structures requires an environment free of oxygen, since oxidation and degradation of material through the activity of microorganisms depend on its presence. One example of the use of analytical chemistry and molecular biology is the identification of oleanane, a compound that deters pests. Up to this point, oleanane appeared to be unique to flowering plants; however, it has now been recovered from sediments dating from the Permian, much earlier than the current dates given for the appearance of the first flowering plants.

Paleobotanists can also study fossil DNA, which can yield a large amount of information, by analyzing and comparing the DNA sequences of extinct plants with those of living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For example, the chemical materials of interest degrade rapidly when exposed to air during their initial isolation, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.

The Major Divisions of Land Plants

The green algae and land plants are grouped together into a subphylum called the Streptophytina, and thus are called Streptophytes. In a further division, land plants are classified into two major groups according to the absence or presence of vascular tissue, as detailed in [\[link\]](#). Plants that lack vascular tissue, which is formed of specialized cells for the transport of water and nutrients, are referred to as **non-vascular plants**. Liverworts, mosses, and hornworts are seedless, non-vascular plants that likely appeared early in land plant evolution. Vascular plants developed a network of cells that conduct water and solutes. The first vascular plants appeared in the late Ordovician and were probably similar to lycophytes, which include club mosses (not to be confused with the mosses) and the pterophytes (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as seedless vascular plants, because they do not produce seeds. The seed plants, or spermatophytes, form the largest group of all existing plants, and hence dominate the landscape. Seed plants include gymnosperms, most notably conifers (Gymnosperms), which produce “naked seeds,” and the most successful of all plants, the flowering plants (Angiosperms). Angiosperms protect their seeds inside chambers at the center of a flower; the walls of the chamber later develop into a fruit.

Note:
Art Connection

STREPTOPHYTES: THE GREEN PLANTS							
Charophytes	Embryophytes: The Land Plants						
	Non Vascular			Vascular			
	Seedless Plants Bryophytes			Seedless Plants		Seed Plants Spermatophytes	
				Lycophytes	Pterophytes		
	Liver- worts	Horn- worts	Mosses	Club Mosses	Whisk Ferns	Gymno- sperms	Angio- sperms
				Quillworts	Horsetails		
				Spike Mosses	Ferns		

This table shows the major divisions of green plants.

Which of the following statements about plant divisions is false?

- a. Lycophytes and pterophytes are seedless vascular plants.
- b. All vascular plants produce seeds.
- c. All nonvascular embryophytes are bryophytes.
- d. Seed plants include angiosperms and gymnosperms.

Section Summary

Land plants acquired traits that made it possible to colonize land and survive out of the water. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte, and the diploid plant called a sporophyte; protection of the embryo, formation of haploid spores in a sporangium, formation of gametes in a gametangium, and an apical meristem. Vascular tissues, roots, leaves, cuticle cover, and a tough outer layer that protects the spores contributed to the adaptation of plants to dry land. Land plants appeared about 500 million years ago in the Ordovician period.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about plant divisions is false?

- a. Lycophytes and pterophytes are seedless vascular plants.
- b. All vascular plants produce seeds.
- c. All nonvascular embryophytes are bryophytes.
- d. Seed plants include angiosperms and gymnosperms.

Solution:

[\[link\]](#) B.

Review Questions

Exercise:

Problem:

The land plants are probably descendants of which of these groups?

- a. green algae
- b. red algae
- c. brown algae
- d. angiosperms

Solution:

A

Exercise:

Problem: Alternation of generations means that plants produce:

- a. only haploid multicellular organisms
- b. only diploid multicellular organisms
- c. only diploid multicellular organisms with single-celled haploid gametes
- d. both haploid and diploid multicellular organisms

Solution:

D

Exercise:

Problem:

Which of the following traits of land plants allows them to grow in height?

- a. alternation of generations
- b. waxy cuticle
- c. tracheids
- d. sporopollenin

Solution:

C

Free Response**Exercise:****Problem:**

Why did land plants lose some of the accessory pigments present in brown and red algae?

Solution:

Sunlight is not filtered by water or other algae on land; therefore, there is no need to collect light at additional wavelengths made available by other pigment coloration.

Exercise:

Problem: What is the difference between extant and extinct?

Solution:

Paleobotanists distinguish between extinct species, which no longer live, and extant species, which are still living.

Glossary

antheridium

male gametangium

archegonium

female gametangium

charophyte

other term for green algae; considered the closest relative of land plants

diplontic

diploid stage is the dominant stage

embryophyte

other name for land plant; embryo is protected and nourished by the sporophyte

extant

still-living species

extinct

no longer existing species

gametangium

structure on the gametophyte in which gametes are produced

haplodiplontic

haploid and diploid stages alternate

haplontic

haploid stage is the dominant stage

heterosporous

produces two types of spores

homosporous
produces one type of spore

megaspore
female spore

microspore
male spore

non-vascular plant
plant that lacks vascular tissue, which is formed of specialized cells for the transport of water and nutrients

seedless vascular plant
plant that does not produce seeds

sporocyte
diploid cell that produces spores by meiosis

sporopollenin
tough polymer surrounding the spore

vascular plant
plant containing a network of cells that conducts water and solutes through the organism

(1104L) Green Algae: Precursors of Land Plants

By the end of this section, you will be able to:

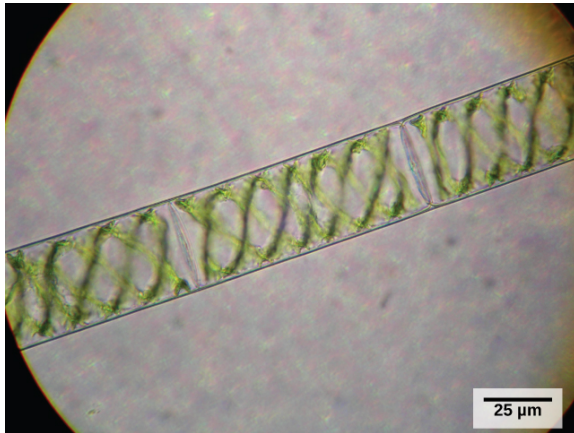
- Describe the traits shared by green algae and land plants
- Explain the reasons why Charales are considered the closest relative to land plants
- Understand that current phylogenetic relationships are reshaped by comparative analysis of DNA sequences

Streptophytes

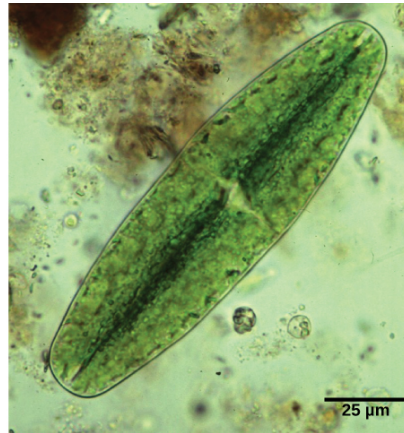
Until recently, all photosynthetic eukaryotes were considered members of the kingdom Plantae. The brown, red, and gold algae, however, have been reassigned to the Protista kingdom. This reclassification was motivated initially by biochemical and cell biological differences between these algal groups and land plants, and is supported by more recent genomic sequencing of species in these groups. What is very clear is that "algae" have evolved more than once. Consequently, land plants and closely related green algae are now part of a new monophyletic group called **Streptophyta**.

The remaining green algae, which belong to a group called Chlorophyta, include more than 7000 different species that live in fresh or brackish water, in seawater, or in snow patches. A few green algae even survive on soil, provided it is covered by a thin film of moisture in which they can live. Periodic dry spells provide a selective advantage to algae that can survive water stress. Some green algae may already be familiar, in particular *Spirogyra* and desmids. Their cells contain chloroplasts that display a dizzying variety of shapes, and their cell walls contain cellulose, as do land plants. Some green algae are single cells, such as *Chlorella* and *Chlamydomonas*, which adds to the ambiguity of green algae classification, because plants are multicellular. Other algae, like *Ulva* (commonly called sea lettuce), form colonies ([\[link\]](#)).

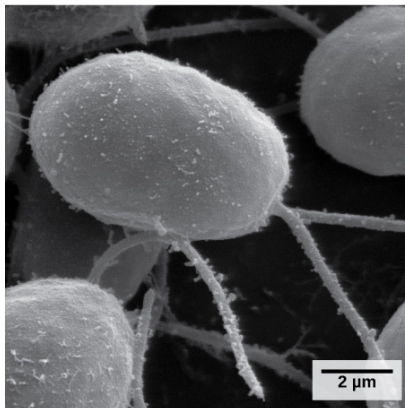
Chlorophyta include (a) *Spirogyra*, (b) desmids, (c) *Chlamydomonas*, and (d) *Ulva*. Desmids and *Chlamydomonas* are single-celled organisms, *Spirogyra* forms chains of cells, and *Ulva* forms colonies resembling leaves (credit b: modification of work by Derek Keats; credit c: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; credit d: modification of work by Holger Krisp; scale-bar data from Matt Russell)



(a) *Spirogyra*



(b) Desmid



(c) *Chlamydomonas*



(d) *Ulva*

Reproduction of Green Algae

Green algae reproduce both asexually, by fragmentation or dispersal of spores, or sexually, by producing gametes that fuse during fertilization. In a single-celled organism such as *Chlamydomonas*, there is no mitosis after

fertilization. In the multicellular *Ulva*, a sporophyte grows by mitosis after fertilization. Both *Chlamydomonas* and *Ulva* produce flagellated gametes.

Charales

Green algae in the order Charales, and the coleochaetes (microscopic green algae that enclose their spores in sporopollenin), are considered the closest living relatives of embryophytes. The Charales can be traced back 420 million years. They live in a range of fresh water habitats and vary in size from a few millimeters to a meter in length. The representative species is *Chara* ([link](#)), often called muskgrass or skunkweed because of its unpleasant smell. Large cells form the thallus: the main stem of the alga. Branches arising from the nodes are made of smaller cells. Male and female reproductive structures are found on the nodes, and the sperm have flagella. Unlike land plants, Charales do not undergo alternation of generations in their lifecycle. Charales exhibit a number of traits that are significant in their adaptation to land life. They produce the compounds lignin and sporopollenin, and form plasmodesmata that connect the cytoplasm of adjacent cells. The egg, and later, the zygote, form in a protected chamber on the parent plant.



The representative alga, *Chara*, is a noxious weed in Florida, where it clogs waterways. (credit: South

New information from recent, extensive DNA sequence analysis of green algae indicates that the Zygnematales are more closely related to the embryophytes than the Charales. The Zygnematales include the familiar genus *Spirogyra*. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between species will change. Clearly, plant biologists have not yet solved the mystery of the origin of land plants.

Section Summary

Green algae share more traits with land plants than other algae, according to structure and DNA analysis. Charales form sporopollenin and precursors of lignin, phragmoplasts, and have flagellated sperm. They do not exhibit alternation of generations.

Review Questions

Exercise:

Problem:

What characteristic of Charales would enable them to survive a dry spell?

- a. sperm with flagella
- b. phragmoplasts
- c. sporopollenin
- d. chlorophyll *a*

Solution:

C

Exercise:

Problem:

Which one of these characteristics is present in land plants and not in Charales?

- a. alternation of generations
- b. flagellated sperm
- c. phragmoplasts
- d. plasmodesmata

Solution:

A

Free Response

Exercise:

Problem:

To an alga, what is the main advantage of producing drought-resistant structures?

Solution:

It allows for survival through periodic droughts and colonization of environments where the supply of water fluctuates.

Glossary

streptophytes

group that includes green algae and land plants

(1104L) Bryophytes

By the end of this section, you will be able to:

- Identify the main characteristics of bryophytes
- Describe the distinguishing traits of liverworts, hornworts, and mosses
- Chart the development of land adaptations in the bryophytes
- Describe the events in the bryophyte lifecycle

Bryophytes are the group of plants that resemble most closely what we know the first land plants looked like. The first bryophytes (liverworts) most likely appeared in the Ordovician period, about 450 million years ago. Because of the lack of lignin and other resistant structures, the likelihood of bryophytes forming fossils is rather small (although they are present). Some spores protected by sporopollenin have survived and are attributed to early bryophytes. By the Silurian period (~420 million years ago), however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

More than 25,000 species of bryophytes thrive in mostly damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They generally lack lignin and do not have actual tracheids (xylem cells specialized for water conduction). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs—including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate—belong to the haploid organism or gametophyte. The sporophyte is barely noticeable. The gametes formed by bryophytes swim with a flagellum, as do gametes in a few of the tracheophytes. The sporangium—the multicellular sexual reproductive structure—is present in bryophytes and absent in the majority of algae. The bryophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Liverworts

Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on Earth and diversified to more than 7000 existing species ([link](#)). Some gametophytes form lobate green structures, as seen in [link](#). The shape is similar to the lobes of the liver, and hence provides the origin of the name given to the phylum.



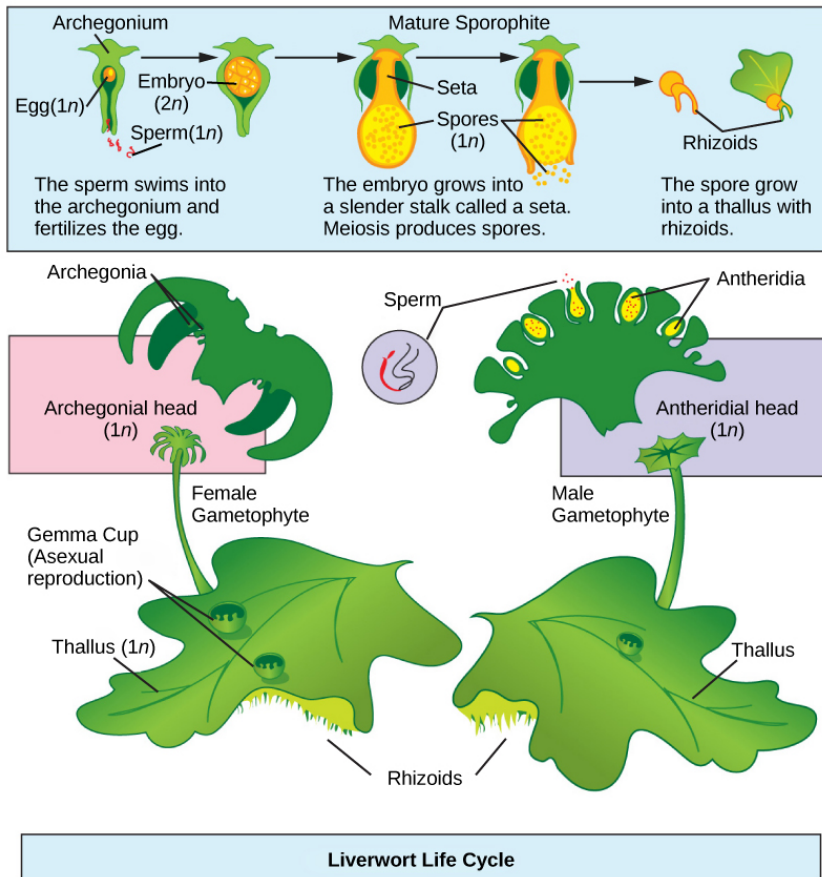
This 1904 drawing shows the variety of forms of Hepaticophyta.



A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata, because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation. [\[link\]](#) represents the lifecycle of a liverwort. The cycle starts with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte. It will give rise, by meiosis, to the next generation of spores. Liverwort plants can also reproduce asexually, by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the **gemmae**—small, intact, complete pieces of plant that are produced in a cup on the

surface of the thallus (shown in [link](#))—are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.



The life cycle of a typical liverwort is shown.
(credit: modification of work by Mariana Ruiz Villareal)

Hornworts

The **hornworts** (*Anthocerotophyta*) belong to the broad bryophyte group. They have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like

sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant ([link](#)).

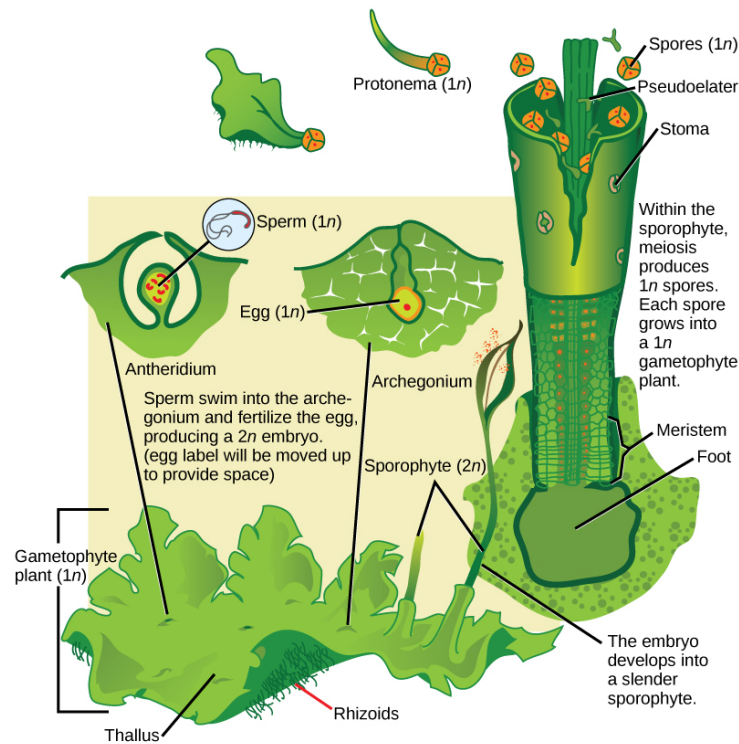


Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)

Stomata appear in the hornworts and are abundant on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.

The lifecycle of hornworts ([link](#)) follows the general pattern of alternation of generations. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. The zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in horsetails, the hornwort pseudoelaters are

single-celled structures. The haploid spores germinate and give rise to the next generation of gametophyte.



The alternation of generation in hornworts is shown. (credit: modification of work by “Smith609”/Wikimedia Commons based on original work by Mariana Ruiz Villareal)

Mosses

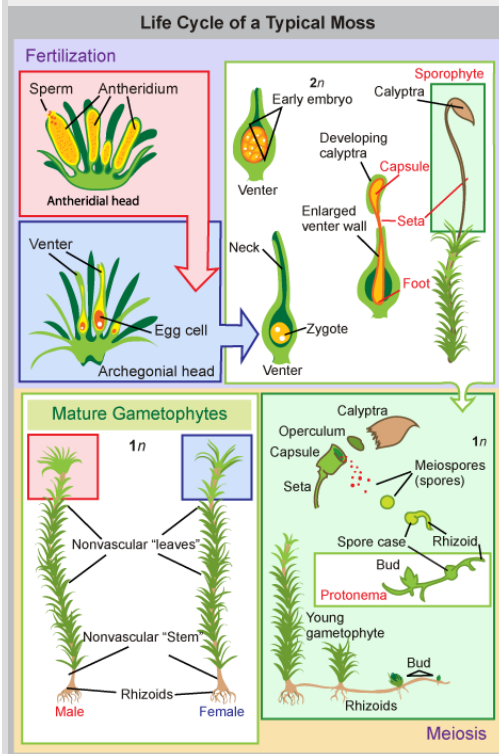
More than 10,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a substrate without penetrating the frozen soil. Mosses slow down

erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts, so these salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the lifecycle. Green, flat structures—resembling true leaves, but lacking vascular tissue—are attached in a spiral to a central stalk. The plants absorb water and nutrients directly through these leaf-like structures. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are clearly adaptations to dry land. For example, stomata are present on the stems of the sporophyte, and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate—whether it is soil, rock, or roof tiles—by multicellular **rhizoids**. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk. The moss lifecycle follows the pattern of alternation of generations as shown in [\[link\]](#). The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a **protonema**—usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

Note:

Art Connection



This illustration shows the life cycle of mosses. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the moss life cycle is false?

- The mature gametophyte is haploid.
- The sporophyte produces haploid spores.
- The calyptra buds to form a mature gametophyte.
- The zygote is housed in the venter.

The slender **seta** (plural, setae), as seen in [\[link\]](#), contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the

sporangium or **capsule**.



This photograph shows the long slender stems, called setae, connected to capsules of the moss *Thamnobryum alopecurum*. (credit: modification of work by Hermann Schachner)

A structure called a **peristome** increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like “teeth”; these open and close depending on moisture levels, and periodically release spores.

Section Summary

Seedless nonvascular plants are small, having the gametophyte as the dominant stage of the lifecycle. Without a vascular system and roots, they absorb water and nutrients on all their exposed surfaces. Collectively known as bryophytes, the three main groups include the liverworts, the hornworts, and the mosses. Liverworts are the most primitive plants and are

closely related to the first land plants. Hornworts developed stomata and possess a single chloroplast per cell. Mosses have simple conductive cells and are attached to the substrate by rhizoids. They colonize harsh habitats and can regain moisture after drying out. The moss sporangium is a complex structure that allows release of spores away from the parent plant.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about the moss life cycle is false?

- a. The mature gametophyte is haploid.
- b. The sporophyte produces haploid spores.
- c. The rhizoid buds to form a mature gametophyte.
- d. The zygote is housed in the venter.

Solution:

[\[link\]](#) C.

Review Questions

Exercise:

Problem:

Which of the following structures is not found in bryophytes?

- a. a cellulose cell wall
 - b. chloroplast
 - c. sporangium
 - d. root
-

Solution:

D

Exercise:

Problem: Stomata appear in which group of plants?

- a. Charales
- b. liverworts
- c. hornworts
- d. mosses

Solution:

C

Exercise:

Problem: The chromosome complement in a moss protonema is:

- a. $1n$
- b. $2n$
- c. $3n$
- d. varies with the size of the protonema

Solution:

A

Exercise:

Problem: Why do mosses grow well in the Arctic tundra?

- a. They grow better at cold temperatures.
- b. They do not require moisture.

- c. They do not have true roots and can grow on hard surfaces.
- d. There are no herbivores in the tundra.

Solution:

C

Free Response

Exercise:

Problem:

In areas where it rains often, mosses grow on roofs. How do mosses survive on roofs without soil?

Solution:

Mosses absorb water and nutrients carried by the rain and do not need soil because they do not derive much nutrition from the soil.

Exercise:

Problem: What are the three classes of bryophytes?

Solution:

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Glossary

capsule
case of the sporangium in mosses

gemma

(plural, gemmae) leaf fragment that spreads for asexual reproduction

hornworts

group of non-vascular plants in which stomata appear

liverworts

most primitive group of the non-vascular plants

mosses

group of bryophytes in which a primitive conductive system appears

peristome

tissue that surrounds the opening of the capsule and allows periodic release of spores

protonema

tangle of single celled filaments that forms from the haploid spore

rhizoids

thin filaments that anchor the plant to the substrate

seta

stalk that supports the capsule in mosses

(1104L) Seedless Vascular Plants

By the end of this section, you will be able to:

- Identify the new traits that first appear in tracheophytes
- Discuss the importance of adaptations to life on land
- Describe the classes of seedless tracheophytes
- Describe the lifecycle of a fern
- Explain the role of seedless vascular plants in the ecosystem

The vascular plants, or **tracheophytes**, are the dominant and most conspicuous group of land plants. More than 260,000 species of tracheophytes represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their ability to spread to all habitats.

Bryophytes may have been successful at the transition from an aquatic habitat to land, but they are still dependent on water for reproduction, and absorb moisture and nutrients through the gametophyte surface. The lack of roots for absorbing water and minerals from the soil, as well as a lack of reinforced conducting cells, limits bryophytes to small sizes. Although they may survive in reasonably dry conditions, they cannot reproduce and expand their habitat range in the absence of water. Vascular plants, on the other hand, can achieve enormous heights, thus competing successfully for light. Photosynthetic organs become leaves, and pipe-like cells or vascular tissues transport water, minerals, and fixed carbon throughout the organism.

In seedless vascular plants, the diploid sporophyte is the dominant phase of the lifecycle. The gametophyte is now an inconspicuous, but still independent, organism. Throughout plant evolution, there is an evident reversal of roles in the dominant phase of the lifecycle. Although all life requires water, seedless vascular plants are especially dependent on water during fertilization, as the sperm must swim on a layer of moisture to reach the female plant (later we will see that seeded plants solved this problem with pollen). This requirement for water explains why ferns and their relatives are more abundant in damp environments.

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue date to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for the storage and long-distance transport of water and nutrients, as well as the transfer of water-soluble growth factors from the organs of synthesis to the target organs. The tissue consists of conducting cells, known as tracheids, and supportive filler tissue, called parenchyma. Xylem conductive cells incorporate the compound **lignin** into their walls, and are thus described as lignified. Lignin itself is a complex polymer that is impermeable to water and confers mechanical strength to vascular tissue. With their rigid cell walls, the xylem cells provide support to the plant and allow it to achieve impressive heights. Tall plants have a selective advantage by being able to reach unfiltered sunlight and disperse their spores or seeds further away, thus expanding their range. By growing higher than other plants, tall trees cast their shadow on shorter plants and limit competition for water and precious nutrients in the soil.

A very old stem



A ~400 fossilized plant stem. Notice the

vascular tissue.

Phloem is the second type of vascular tissue; it transports sugars, proteins, and other solutes throughout the plant. Phloem cells are divided into sieve elements (conducting cells) and cells that support the sieve elements. Together, xylem and phloem tissues form the vascular system of plants.

Roots: Support for the Plant

Roots are not well preserved in the fossil record. Nevertheless, it seems that roots appeared later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Thin rhizoids attached bryophytes to the substrate, but these rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb substantial amounts of water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep into the soil to reach sources of water also stabilizes trees by acting as a ballast or anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae, which benefit the plant by greatly increasing the surface area for absorption of water and soil minerals and nutrients.

Leaves, Sporophylls, and Strobili

A third innovation marks the seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved their photosynthetic efficiency. Leaves capture more sunlight with their increased surface area by employing more chloroplasts to trap light energy and convert it to chemical energy, which is then used to fix atmospheric carbon dioxide into carbohydrates. The carbohydrates are exported to the rest of the plant by the conductive cells of phloem tissue.

The existence of two types of morphology suggests that leaves evolved independently in several groups of plants. The first type of leaf is the **microphyll**, or “little leaf,” which can be dated to 350 million years ago in the late Silurian. A microphyll is small and has a simple vascular system. A single unbranched **vein**—a bundle of vascular tissue made of xylem and phloem—runs through the center of the leaf. Microphylls may have originated from the flattening of lateral branches, or from sporangia that lost their reproductive capabilities. Microphylls are present in the club mosses and probably preceded the development of **megaphylls**, or “big leaves”, which are larger leaves with a pattern of branching veins. Megaphylls most likely appeared independently several times during the course of evolution. Their complex networks of veins suggest that several branches may have combined into a flattened organ, with the gaps between the branches being filled with photosynthetic tissue.

Ferns and Other Seedless Vascular Plants

By the late Devonian period, plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period, swamp forests of club mosses and horsetails—some specimens reaching heights of more than 30 m (100 ft)—covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name and that are currently being burned to generate a significant of the world's electricity. In seedless vascular plants, the sporophyte became the dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless tracheophytes include club mosses, horsetails, ferns, and whisk ferns.

Phylum Lycopodiophyta: Club Mosses

The **club mosses**, or phylum **Lycopodiophyta**, are the earliest group of seedless vascular plants. They dominated the landscape of the

Carboniferous, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and microphylls ([link](#)). The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (*Isoetales*), the club mosses (*Lycopodiales*), and spike mosses (*Selaginellales*), none of which are true mosses or bryophytes.

Lycophytes follow the pattern of alternation of generations seen in the bryophytes, except that the sporophyte is the major stage of the lifecycle. The gametophytes do not depend on the sporophyte for nutrients. Some gametophytes develop underground and form mycorrhizal associations with fungi. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name. Lycophytes can be homosporous or heterosporous.



In the club mosses such as
Lycopodium clavatum,
sporangia are arranged in
clusters called strobili. (credit:
Cory Zanker)

Phylum Monilophyta: Class Equisetopsida (Horsetails)

Horsetails, whisk ferns and ferns belong to the phylum Monilophyta, with **horsetails** placed in the Class Equisetopsida. The single genus *Equisetum* is the survivor of a large group of plants, known as ArthropHYta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes ([\[link\]](#)).



Horsetails thrive in a marsh.
(credit: Myriam Feldman)

The stem of a horsetail is characterized by the presence of joints or nodes, hence the name ArthropHYta (arthro- = "joint"; -phyta = "plant"). Leaves and branches come out as whorls from the evenly spaced joints. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem ([\[link\]](#)).



Thin leaves originating at the joints are noticeable on the horsetail plant.

Horsetails were once used as scrubbing brushes and were nicknamed scouring brushes. (credit: Myriam Feldman)

Silica collects in the epidermal cells, contributing to the stiffness of horsetail plants. Underground stems known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous and produce bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

While most ferns form large leaves and branching roots, the **whisk ferns**, Class Psilotopsida, lack both roots and leaves, probably lost by reduction.

Photosynthesis takes place in their green stems, and small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns were considered an early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both vascular tissue and roots through evolution, and is more closely related to ferns.



The whisk fern *Psilotum nudum* has conspicuous green stems with knob-shaped sporangia.
(credit: Forest & Kim Starr)

Phylum Monilophyta: Class Psilotopsida (Ferns)

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants. They are considered the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. More than 20,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

The dominant stage of the lifecycle of a fern is the sporophyte, which consists of large compound leaves called fronds. Fronds fulfill a double role; they are photosynthetic organs that also carry reproductive organs. The stem may be buried underground as a rhizome, from which roots grow to absorb water and nutrients from the soil; or, they may grow above ground as a trunk in tree ferns ([link](#)).



Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone)

The tip of a developing fern frond is rolled into a crozier, or fiddlehead ([link](#)**a** and [link](#)**b**). Fiddleheads unroll as the frond develops.

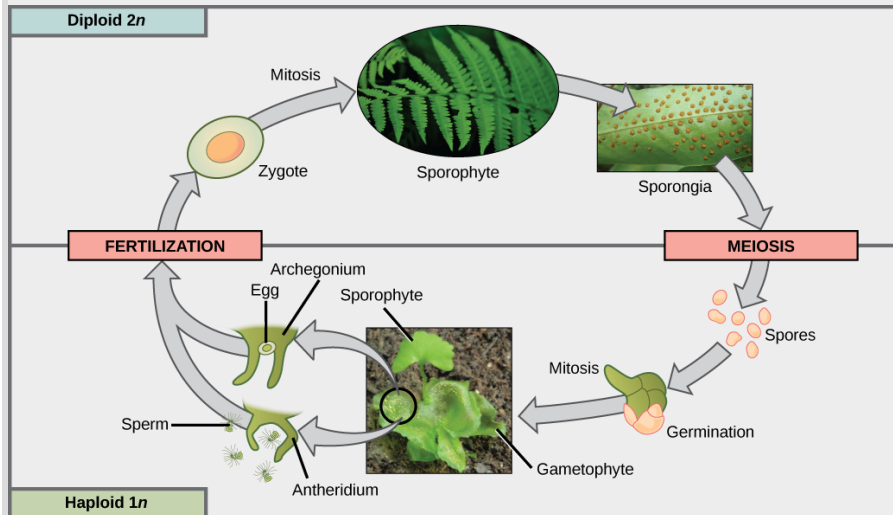


Crozier, or fiddleheads, are the tips of fern fronds. (credit a: modification of work by Cory Zanker; credit b: modification of work by Myriam Feldman)

The lifecycle of a fern is depicted in [\[link\]](#).

Note:

Art Connection



This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)

Which of the following statements about the fern life cycle is false?

- a. Sporangia produce haploid spores.
- b. The sporophyte grows from a gametophyte.

- c. The sporophyte is diploid and the gametophyte is haploid.
- d. Sporangia form on the underside of the gametophyte.

Note:

Link to Learning



To see an animation of the lifecycle of a fern and to test your knowledge, go to the [website](#).

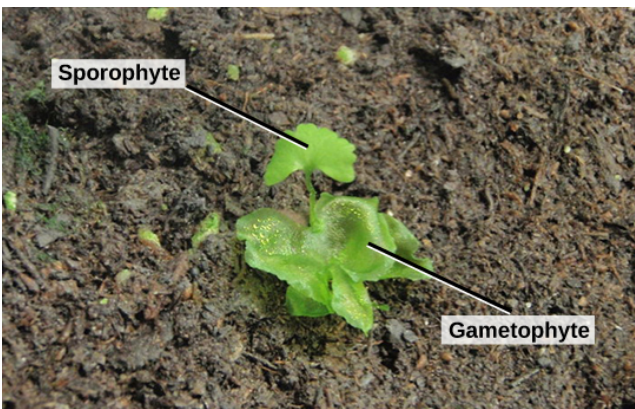
Most ferns produce the same type of spores and are therefore homosporous. The diploid sporophyte is the most conspicuous stage of the lifecycle. On the underside of its mature fronds, sori (singular, sorus) form as small clusters where sporangia develop ([link](#)).



Sori appear as small bumps on the underside of a fern frond. (credit:

Myriam Feldman)

Inside the sori, spores are produced by meiosis and released into the air. Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids ([link](#)).



Shown here are a young sporophyte (upper part of image) and a heart-shaped gametophyte (bottom part of image). (credit: modification of work by "Vlmastra"/Wikimedia Commons)

The inconspicuous gametophyte harbors both sex gametangia. Flagellated sperm released from the antheridium swim on a wet surface to the archegonium, where the egg is fertilized. The newly formed zygote grows into a sporophyte that emerges from the gametophyte and grows by mitosis into the next generation sporophyte.

Note:**Career Connection****Landscape Designer**

Looking at the well-laid parterres of flowers and fountains in the grounds of royal castles and historic houses of Europe, it's clear that the gardens' creators knew about more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States' tradition. A prime example of early American classical design is Monticello: Thomas Jefferson's private estate. Among his many interests, Jefferson maintained a strong passion for botany.

Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L'Enfant's design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens. The restoration of natural places encroached on by human intervention, such as wetlands, also requires the expertise of a landscape designer.

With such an array of necessary skills, a landscape designer's education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. Mosses and ferns will thrive in a shaded area, where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of individual plants must be taken into account, to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.



This landscaped border at a college campus was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

The Importance of Seedless Vascular Plants

Mosses and liverworts are often the first macroscopic organisms to colonize an area, both in a primary succession—where bare land is settled for the first time by living organisms—or in a secondary succession, where soil remains intact after a catastrophic event wipes out many existing species. Their spores are carried by the wind, birds, or insects. Once mosses and liverworts are established, they provide food and shelter for other species. In a hostile environment, like the tundra where the soil is frozen, bryophytes grow well because they do not have roots and can dry and rehydrate rapidly once water is again available. Mosses are at the base of the food chain in the tundra biome. Many species—from small insects to musk oxen and reindeer—depend on mosses for food. In turn, predators feed on the herbivores, which are the primary consumers. Some reports indicate that bryophytes make the soil more amenable to colonization by other plants. Because they establish symbiotic relationships with nitrogen-fixing cyanobacteria, mosses replenish the soil with nitrogen.

At the end of the nineteenth century, scientists observed that lichens and mosses were becoming increasingly rare in urban and suburban areas. Since bryophytes have neither a root system for absorption of water and nutrients, nor a cuticle layer that protects them from desiccation, pollutants in rainwater readily penetrate their tissues; they absorb moisture and nutrients through their entire exposed surfaces. Therefore, pollutants dissolved in rainwater penetrate plant tissues readily and have a larger impact on mosses than on other plants. The disappearance of mosses can be considered a bioindicator for the level of pollution in the environment.

Ferns contribute to the environment by promoting the weathering of rock, accelerating the formation of topsoil, and slowing down erosion by spreading rhizomes in the soil. The water ferns of the genus *Azolla* harbor nitrogen-fixing cyanobacteria and restore this important nutrient to aquatic habitats.

Seedless plants have historically played a role in human life through uses as tools, fuel, and medicine. Dried **peat moss**, *Sphagnum*, is commonly used as fuel in some parts of Europe and is considered a renewable resource. *Sphagnum* bogs ([\[link\]](#)) are cultivated with cranberry and blueberry bushes. The ability of *Sphagnum* to hold moisture makes the moss a common soil conditioner. Florists use blocks of *Sphagnum* to maintain moisture for floral arrangements.



Sphagnum acutifolium is dried peat moss and can be used as

fuel. (credit: Ken Goulding)

The attractive fronds of ferns make them a favorite ornamental plant. Because they thrive in low light, they are well suited as house plants. More importantly, fiddleheads are a traditional spring food of Native Americans in the Pacific Northwest, and are popular as a side dish in French cuisine. The licorice fern, *Polypodium glycyrrhiza*, is part of the diet of the Pacific Northwest coastal tribes, owing in part to the sweetness of its rhizomes. It has a faint licorice taste and serves as a sweetener. The rhizome also figures in the pharmacopeia of Native Americans for its medicinal properties and is used as a remedy for sore throat.

Note:

Link to Learning



Go to this [website](#) to learn how to identify fern species based upon their fiddleheads.

By far the greatest impact of seedless vascular plants on human life, however, comes from their extinct progenitors. The tall club mosses, horsetails, and tree-like ferns that flourished in the swampy forests of the Carboniferous period gave rise to large deposits of coal throughout the world. Coal provided an abundant source of energy during the Industrial Revolution, which had tremendous consequences on human societies, including rapid technological progress and growth of large cities, as well as

the degradation of the environment. Coal is still a prime source of energy and also a major contributor to global warming.

Section Summary

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the development of the vascular system, there appeared leaves to act as large photosynthetic organs, and roots to access water from the ground. Small uncomplicated leaves are microphylls. Large leaves with vein patterns are megaphylls. Modified leaves that bear sporangia are sporophylls. Some sporophylls are arranged in cone structures called strobili.

The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; and horsetails and ferns. Ferns are the most advanced group of seedless vascular plants. They are distinguished by large leaves called fronds and small sporangia-containing structures called sori, which are found on the underside of the fronds.

Mosses play an essential role in the balance of the ecosystems; they are pioneering species that colonize bare or devastated environments and make it possible for a succession to occur. They contribute to the enrichment of the soil and provide shelter and nutrients for animals in hostile environments. Mosses and ferns can be used as fuels and serve culinary, medical, and decorative purposes.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about the fern life cycle is false?

- a. Sporangia produce haploid spores.

- b. The sporophyte grows from a gametophyte.
- c. The sporophyte is diploid and the gametophyte is haploid.
- d. Sporangia form on the underside of the gametophyte.

Solution:

[\[link\]](#) D.

Review Questions

Exercise:

Problem: Microphylls are characteristic of which types of plants?

- a. mosses
- b. liverworts
- c. club mosses
- d. ferns

Solution:

C

Exercise:

Problem:

A plant in the understory of a forest displays a segmented stem and slender leaves arranged in a whorl. It is probably a _____.

- a. club moss
- b. whisk fern
- c. fern
- d. horsetail

Solution:

D

Exercise:

Problem:

The following structures are found on the underside of fern leaves and contain sporangia:

- a. sori
- b. rhizomes
- c. megaphylls
- d. microphylls

Solution:

A

Exercise:

Problem: The dominant organism in fern is the _____.

- a. sperm
- b. spore
- c. gamete
- d. sporophyte

Solution:

D

Exercise:

Problem: What seedless plant is a renewable source of energy?

- a. club moss
- b. horsetail
- c. sphagnum moss
- d. fern

Solution:

C

Exercise:

Problem: How do mosses contribute to returning nitrogen to the soil?

- a. Mosses fix nitrogen from the air.
- b. Mosses harbor cyanobacteria that fix nitrogen.
- c. Mosses die and return nitrogen to the soil.
- d. Mosses decompose rocks and release nitrogen.

Solution:

D

Free Response

Exercise:

Problem:

How did the development of a vascular system contribute to the increase in size of plants?

Solution:

Plants became able to transport water and nutrients and not be limited by rates of diffusion. Vascularization allowed the development of

leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Exercise:

Problem:

Which plant is considered the most advanced seedless vascular plant and why?

Solution:

Ferns are considered the most advanced seedless vascular plants, because they display characteristics commonly observed in seed plants—they form large leaves and branching roots.

Glossary

adventitious

describes an organ that grows in an unusual place, such as a roots growing from the side of a stem

club mosses

earliest group of seedless vascular plants

fern

seedless vascular plant that produces large fronds; the most advanced group of seedless vascular plants

horsetail

seedless vascular plant characterized by joints

lignin

complex polymer impermeable to water

lycophyte

club moss

megaphyll

larger leaves with a pattern of branching veins

microphyll

small size and simple vascular system with a single unbranched vein

peat moss

Sphagnum

phloem

tissue responsible for transport of sugars, proteins, and other solutes

sporophyll

leaf modified structurally to bear sporangia

strobili

cone-like structures that contain the sporangia

tracheophyte

vascular plant

vein

bundle of vascular tissue made of xylem and phloem

whisk fern

seedless vascular plant that lost roots and leaves by reduction

xylem

tissue responsible for long-distance transport of water and nutrients